

DETERMINING MINIMUM POPULATION SIZE FOR RECOVERY OF THE BLACK-FOOTED FERRET

Craig R. Groves^{1,2} and Tim W. Clark¹

ABSTRACT.—A minimum viable population (MVP) size is estimated for the critically endangered black-footed ferret by examining five basic methods: experiments, biogeographic patterns, theoretical models, simulation models, and genetic considerations. Each method is evaluated for its applicability to the ferret and endangered species in general with two criteria in mind: (1) potential research impacts to target species and (2) the value of scientific accuracy and precision in relation to short-term conservation needs. For the black-footed ferret, the genetic method proved to be the most useful, resulting in an MVP estimate of about 200 ferrets for maintenance of short-term fitness. For most endangered species, a combination of the simulation and genetic methods will probably yield the best estimate of MVP size. MVP estimates have direct implications for future research, management, and recovery efforts of endangered species.

Following the 1981 discovery of the critically endangered black-footed ferret (*Mustela nigripes*) in northwestern Wyoming, the only population of the species known, two primary goals of a ferret study were established: (1) conservation of the population and (2) recovery of the species (Clark 1984a). Estimation of population parameters such as distribution, birth rate, death rate, and immigration/emigration was a major objective. In addition to providing valuable life history data for the ferret, estimating these parameters would enable us to address a key question: What is the minimum ferret population size necessary for the species to persist (i.e., avoid extinction)? Because of the apparent small size of the Wyoming population in 1981, the answer was paramount for successful conservation and, ultimately, species recovery.

The minimum population size concept for species conservation was recently introduced by Shaffer (1981), with potentially significant implications for endangered species programs. Although many endangered species studies have been conducted, few have tried to estimate minimum population sizes (Shaffer 1978, 1981, Lacava and Hughes 1984, Salwasser et al. 1984). Although USDA Forest Service regulations require that minimum viable populations of endangered species be maintained on Forest Service lands, these population numbers are not estimated but are instead routinely established as those levels specified in recovery plans

(Lacava and Hughes 1984). In this paper, we estimate minimum ferret population numbers and, as a corollary, minimum area requirements. Our purpose is to establish guidelines for future ferret research and management and to provide impetus, direction, and encouragement to other endangered species programs to use the concept of minimum population size.

CONCEPT OF MINIMUM VIABLE POPULATION SIZE

The notion of a required minimum population size for species conservation was first embodied by Shaffer (1981) in his concept of minimum viable population (MVP) size. He defined the MVP for a species as the smallest isolated population having a 99% chance of remaining extant for 1000 years despite foreseeable effects of four types of stochastic events: (1) demographic stochasticity, or the chance events in the survival and reproductive fitness of a finite number of individuals; (2) environmental stochasticity, or perturbations due to habitat parameters, competitors, predators, and disease; (3) natural catastrophes, such as randomly occurring floods, fires, droughts, etc.; and (4) genetic perturbations resulting from changes in gene frequency. Shaffer (1981) stressed the tentative nature of his definition and emphasized the importance of defining MVP with explicit but flexible criteria such as time frame and survival probability. For

¹Department of Biological Sciences, Idaho State University, Pocatello, Idaho 83209.

²Present address: The Nature Conservancy, 4696 Overland Road, Suite 518, Boise, Idaho 83705.

example, the survival probability could be set at 95% or any other level, and the time frame could be shortened or lengthened as appropriate for planning needs.

Shaffer (1981) proposed five basic methods for determining MVP size: experiments, biogeographic patterns, theoretical models, simulation models, and genetic considerations. In the next section, we elaborate on the application and utility of each method for estimating MVP size for ferrets in particular and endangered species in general. The usefulness of each method is pragmatically evaluated relative to: (1) acceptable levels of potential research impacts on target species and (2) the real value of scientific accuracy and precision in relation to short-term conservation needs. In endangered species recovery work, these two concerns must be addressed.

The MVP concept is a rapidly evolving one. In late 1984, the Forest Service and other agencies sponsored a workshop to provide a state-of-the-art review of the MVP issue (M. L. Shaffer, personal communication). A major purpose of the workshop was to consider revisions of Forest Service procedures for estimating MVP size. The primary focus of the workshop was a discussion of the relative importance of demographic, environmental, and genetic variability in determining minimum population numbers as well as the development of new simulation and analytical models for estimating MVP size. Proceedings of this workshop, which will be published in 1986, may provide additional methods not discussed in this paper and/or may suggest revisions of methods outlined and discussed below for estimating MVP sizes of endangered species.

DETERMINING MVP SIZE

Experiments

This method establishes isolated populations of species and monitors their population dynamics through time. If censusing can be accomplished without stressful manipulation of individuals (as can occur in a capture/recapture program), this approach requires only low levels of research activities. The only necessary data are population numbers and the area inhabited over a specific time period (i.e., time frame in MVP definition).

Determining MVP via experimental methods brings up three concerns. Although methodo-

logically simple, this approach is not plausible for many species, particularly endangered ones. First, for many endangered species, there exists no possibility of studying several isolated populations. In the case of the ferret, there is only one known population, and consequently there is no way to measure variability in persistence of different-sized, isolated populations. Second, time is not an unlimited resource in most endangered species studies. The years necessary to monitor persistence of populations for MVP estimates are simply not available for most endangered species. Lastly, many wildlife species cannot be censused sufficiently without some type of mark/recapture program. These techniques can have negative research impacts (e.g., trap mortality) that some endangered species projects may not be willing to risk, particularly in the early stages. Because endangered species programs in general possess high levels of uncertainty, there may be hesitancy to increase uncertainty to even greater levels (Clark 1984b). Such has been the case in the Wyoming ferret project, where one research team chose initially not to employ mark/recapture and radio telemetry procedures until other methods proved the population large enough to withstand some stress (Clark 1981).

The experimental method could prove useful when extensive population data are available prior to a species becoming endangered. For example, mountain goat (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*) populations have been reintroduced to several sites in the western United States in recent years (Rideout 1978, Wishart 1978). If wildlife researchers monitor the dynamics of these introduced populations, the data should eventually allow them to estimate MVP sizes for these species. Such information would be useful not only for future translocations of these species' populations but also for management if, for example, an isolated population showed a decline in numbers.

Biogeographic Patterns

By studying the distribution patterns of species occupying patchy or insular habitats, an estimate of MVP size and minimum area requirements can be obtained. However, populations examined should be in equilibrium and their approximate period of isolation known (Shaffer 1981). Under these conditions, researchers can estimate the smallest area inhabited by a species

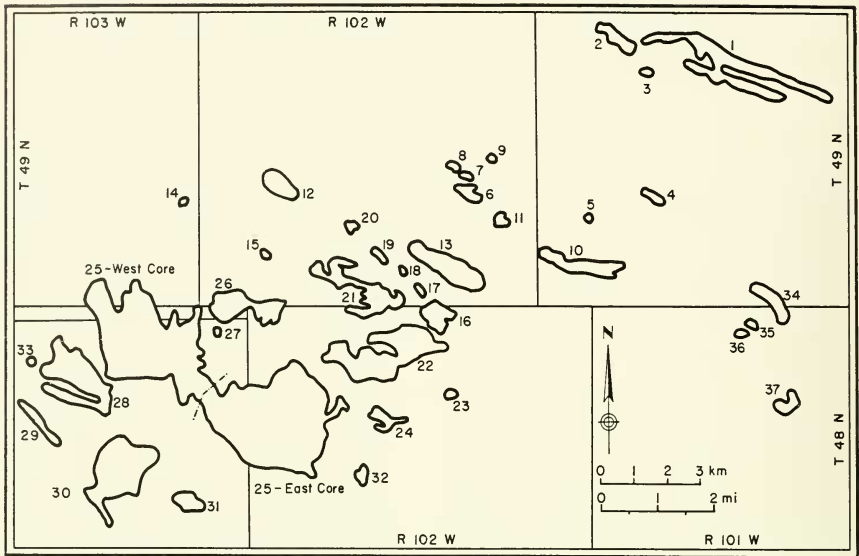


Fig. 1. Distribution of 37 white-tailed prairie dog colonies on the Wyoming black-footed ferret study area, 1981-1984.

and the percentage of patches of a particular size that a species occupies. The smallest population that has persisted over an extensive time period can then provide a first estimate of MVP size.

Because the ferret occupies a patchy habitat (i.e., prairie dog colonies with relatively discrete boundaries, Fig. 1), this approach can be applied, at least in part, to the Wyoming population. Old time trappers have reported catching ferrets in the 1920s and 1930s on the Wyoming study area, thus indicating that ferrets may have occupied the site for at least 50 years. Extinction and recolonization, although unlikely, could have occurred during this period. Population censuses over the last four years (Clark 1986) suggest that the Wyoming ferret population is not in equilibrium but is increasing. As a result, more sophisticated census techniques (e.g., mark/recapture) are being used, leading to more precise and accurate population data. In the future, researchers should thus be able to determine with some degree of confidence whether the Wyoming population is reaching an equilibrium density.

If the Wyoming ferret population stabilizes in numbers, then data from this population will provide the first field assessment of MVP size

and minimum area requirements for the species. However, due to the time required to obtain these data, the biogeographical method will not likely be useful for short-term management decisions concerning MVP size. Nevertheless, useful information on minimum area requirements can be gleaned from the biogeographical approach.

In the short run, researchers will need to decide what size of an area is necessary for ferret reintroduction or translocation for recovery planning (Forrest et al. 1985; Houston et al. 1986). A recommendation for an area larger than the Wyoming site is warranted for two reasons. First, two habitat patches (e.g., Wyoming and South Dakota) of equal size may not be the same in habitat quality. For example, Wyoming ferrets occur on white-tailed prairie dog (*Cynomys leucurus*) colonies, whereas a South Dakota population of ferrets occupied black-tailed prairie dog (*C. ludovicianus*) colonies (Hillman and Clark 1980). White-tails usually form small, sparsely populated colonies; black-tails form large, densely populated colonies (Hoogland 1981). Consequently, a habitat patch that is large enough in one part of the range of the species might be insufficient in another due to differ-

ences in habitat quality. Second, nothing is known about the frequency with which ferret populations go extinct on habitat patches of various sizes. Therefore, it would be inadvisable to rely on the size of the Wyoming study area as an exemplary model of area requirements for black-footed ferrets.

Although the biogeographical approach cannot be used for endangered species with contiguous distributions, it is applicable for species with insular or patchy distributions. Its greatest use should be for endangered species that occupy patches of different size and similar quality and for which data on population numbers and isolation periods are available. For example, the Shoshone sculpin (*Cottus greeni*) is restricted to different-sized spring systems along a 45-km stretch of the Snake River in south central Idaho (Wallace et al. 1984). Relative and absolute densities of the sculpin in many of these spring systems were determined during a status survey in 1980–1981 (J. Griffith, personal communication). By monitoring the persistence of these spring populations of this short-lived species over the next several years, researchers could estimate MVP size and minimum area requirements for this species.

Theoretical Models

Although there are several theoretical models that predict extinction probabilities and times for a population, most are too complex for the simple data bases of endangered species. The theory of island biogeography (MacArthur and Wilson 1967), however, has received considerable attention in the conservation field. Though originally developed in relation to true oceanic islands, this theory has been widely applied to continental habitat "islands" or patches (e.g., Brown 1971). The theory's greatest potential application has been in the design of nature preserves for maintenance of species diversity (for review, see Margules et al. 1982). Much less attention has been devoted to those aspects of the theory that predict the distribution of a single, insular species (Smith 1974, Fritz 1979).

Because the Wyoming ferret population is located on a large habitat "island" (i.e., prairie dog colony complex in Fig. 1), we employed the T_k model of island biogeography to predict probabilities of successful colonization and times to extinction for the ferret. Regarding the Wyoming prairie dog colony complex as a single is-

land is supported by three lines of evidence: (1) several prairie dog colonies at the Wyoming site contained at one time or another only one adult ferret, suggesting that interbreeding of ferrets among prairie dog colonies is occurring, (2) movement data reveal that ferrets range an average of 2.5 km between colonies, with the maximum intercolony movement being 5.7 km (Forrest et al. 1985), and (3) aerial and ground surveys indicate that potential ferret habitat declines significantly beyond the boundaries of this single colony complex, strongly suggesting that these ferrets represent a distinct, isolated population.

Data required in the T_k model are carrying capacity (K), per capita birth rates (λ), and per capita death rates (μ). Direct observations of ferret litters in Wyoming indicated an average litter size of 3.4, or 1.7 female young per adult female (Forrest et al., in manuscript). We assumed that the sex ratio approximated unity, natality did not vary with age, and all females bred. No data on juvenile mortality were available for ferrets; data from other mustelids indicated a medium (60%) to high (80%) rate of juvenile mortality (King 1980, *M. nivalis*; King 1983, *M. erminea*; K. C. Walton personal communication, *M. putorius*). We used a juvenile mortality rate of 0.7, resulting in a λ of 0.5. As with juvenile mortality rates, no data on adult mortality rates were available for ferrets. Data from other mustelids indicated adult mortality ranged from 15%–25% for *Martes pennanti* (Kelly 1977), *M. americana* (Strickland et al. 1982), and *Mustela erminea* (Stroganov 1937), although King (1980) reported mortality rates of 80%–90% for *M. nivalis*. We varied adult mortality (μ) for ferrets from 0.2 to 0.4.

The probability of ferret populations of size n reaching a size where the probability of extinction is nearly zero was calculated by

$$P \sim 1 - (\mu/\lambda)^n$$

where μ and λ are the per capita death and birth rates, respectively (MacArthur and Wilson 1967, Richter-Dyn and Goel 1972). Two results emerged from this analysis (Table 1). First, as μ/λ decreases, the number of female ferrets needed to colonize an area successfully decreases for a given probability. Second, as the number of breeding females increases, a higher μ/λ can still be tolerated with a high probability of successful colonization. These results have a practical application in the reintroduction of

TABLE 1. Probability of a female black-footed ferret population of size n successfully colonizing and reaching carrying capacity. For a birth rate (λ) of 0.5 and a death rate (μ) varied from 0.2 to 0.4, the resulting μ/λ ranges from 0.4 to 0.8.

Population size (n)	Death rate/birth rate ratio (μ/λ)					
	0.9	0.8	0.7	0.6	0.5	0.4
5	0.41	0.67	0.83	0.92	0.97	0.99
10	0.65	0.89	0.97	0.99		
15	0.79	0.96	0.99			
20	0.88	0.99				
30	0.96					
40	0.98					
50	0.99					

black-footed ferrets. For example, if μ/λ is conservatively estimated to be 0.9, these data suggest that at least 15 females will be needed for a reintroduction that has an 80% chance of succeeding. As more accurate birth and death rates are estimated for the Wyoming ferrets, this type of analysis will become even more useful for assessing the number of animals needed for translocations.

We also calculated extinction times for an established population of ferrets (Table 2). These values (T_k) were estimated by the MacArthur and Wilson (1967) equations

$$T_k \sim T_1 \frac{\lambda}{\lambda - \mu} \quad \text{where}$$

$$T_1 = \sum_{i=1}^k (\lambda/\mu)^i \cdot (1/i\lambda)$$

As the death rate to birth rate ratio (μ/λ) increases, the time to extinction (T_k) decreases. For a given μ/λ , T_k increases as the carrying capacity (K) increases. Assuming that the carrying capacity of the Wyoming ferret population is approximately 40 adults (Forrest et al. 1985) and that μ/λ equals 0.8, the time to extinction for this population as predicted by the T_k model would be about 1,000 years. Data from Table 1 show that this population of 40 (20 females, 20 males) with a death rate/birth rate ratio of 0.8 would have about a 99% chance of successful colonization and conversely less than a 1% probability of extinction. Thus, a population of 40 adult ferrets should be a reasonable first estimate of MVP size as predicted by the T_k model. If we assume that there is a constant average density of ferrets across the study area of 1/50 ha (Forrest et al. 1985), this MVP estimate would result in a minimum area requirement of 2,000 ha. In actuality,

TABLE 2. Times to extinction (T_k) for black-footed ferret populations with a carrying capacity (K) of 40 and 50, and birth (λ)/death (μ) rates varied as shown. See text for details.

	λ	μ	μ/λ	T_k (years)
K = 40	0.5	0.2	0.4	1.0×10^{15}
	0.5	0.3	0.6	3.0×10^7
	0.5	0.4	0.8	1.0×10^3
K = 50	0.5	0.2	0.4	8.0×10^{18}
	0.5	0.3	0.6	5.0×10^9
	0.5	0.4	0.8	5.0×10^4

because prairie dog densities vary in this habitat (Clark et al. 1985), the 2,000 ha figure is low.

For endangered species with insular or patchy distributions, the theory of island biogeography can be a useful tool for estimating MVP size if data on birth and death rates are available. The T_k model is a mathematically simple one that assumes limited exponential growth, either birth or death rates that vary linearly with density, no age-specific variance of birth and death rates, and a constant environment. Nevertheless, the T_k model has at least two serious drawbacks: (1) it ignores inbreeding depression (see genetic considerations), which may be important in small populations, and (2) violation of the model assumptions decreases the time to extinction (T_k), thus producing what may be overly optimistic T_k values (Shaffer and Samson 1985). For the ferret, there is good evidence that not all females breed and that natality varies with age (Forrest et al., in manuscript), thereby violating two assumptions of the model. The degree to which these violations may decrease extinction times is unknown.

Other researchers have criticized all aspects of island biogeography theory, the T_k model included, claiming it remains essentially unsubstantiated (Gilbert 1980, Margules et al. 1982). Despite these criticisms, several studies have shown good agreement between model predictions and field observations. Crowell (1973) reported good accordance between observed and predicted times to extinction for mice introduced to islands. Similarly, Smith (1974, 1980) and Fritz (1979) predicted times to extinction that appeared to explain satisfactorily local distributions of pikas (*Ochotona princeps*) and spruce grouse (*Canachites canadensis*). We suggest that the T_k model of island biogeography remains a useful one that should be used in conjunction with other methods to estimate MVP size and area requirements.

Simulation Models

Computer simulations may be the most useful method to estimate MVP size and minimum area requirements. Except for theoretical models like the T_k of island biogeography, computer models provide the only method in which a probability value for survival can be attached to the MVP estimate. In addition, these models are not confined to the mathematical assumptions of analytical models (e.g., density dependent natality or mortality rates, lack of age structure) and provide a flexible mechanism for assessing the sensitivity of MVP estimates to changes in certain population parameters.

Shaffer (1978) employed the simulation approach to estimate MVP size and minimum area requirements for the grizzly bear (*Ursus arctos*) in Yellowstone National Park. This simulation evaluated the effects of both demographic and environmental stochasticity and also indicated which population parameters were most likely to affect changes in survival probability. Watts and Conley (1981) used both stochastic and deterministic models to predict survival and extinction probabilities for a remnant population of bighorn sheep in the southwestern United States. Their simulations evaluated the effects of demographic but not environmental stochasticity. Although an estimate of MVP size was not an explicit result of their effort, it could have been obtained from their simulations.

The major disadvantage of the simulation approach is the extensive population data it requires. Minimum data requirements are the mean and variance of age-specific and sex-specific natality/mortality rates, age structure, sex ratio, and the relationship of these variables to density (Shaffer 1981). For most species, obtaining these data requires an extensive and intensive mark/recapture and/or radio telemetry effort over several years. In his grizzly bear simulation, Shaffer (1978) used the 12-year data base of Craighead et al. (1974). Such extensive data for any wildlife species are the exception, not the rule. However, for some species in which data are lacking, it should be feasible to substitute data from a closely related (congeneric) species into the simulation.

The black-footed ferret is a case in point. Although some natality and sex ratio data are available (Forrest et al., in manuscript), mortality data are not. With ferret data on natality and steppe polecat (*M. evermanni*) data on mortal-

ity, Shaffer (personal communication) simulated some preliminary estimates of MVP size for the ferret. Work is now in progress to refine these simulations, which will take into account both demographic and environmental stochasticity. As the Wyoming ferret study proceeds, more age- and sex-specific natality/mortality data may become available to incorporate into the simulation. For short-term management needs, however, a MVP estimate by simulation using data from a closely related species should suffice for the black-footed ferret.

Although not directly useful in estimating MVP size, simulation models based on bioenergetics are useful in estimating minimum area requirements. Two such models exist for the ferret. One model estimates gestation, lactation, and growth energy requirements for one female ferret and her young (Stromberg et al. 1983); the other estimates energy requirements based on experimental feeding studies of steppe polecats and observed activity patterns of the Wyoming ferrets (Powell et al. 1985). Both models indicate the number of prairie dogs required to support a given population of ferrets. Combined with estimates of MVP size, data from these models are helpful in estimating minimum area requirements for the ferret, assuming that prey (prairie dog) densities can be measured and that there is a close correspondence between prey density and availability.

Computer simulations, though realistic in some aspects, cannot incorporate all the behavioral and ecological adaptations of every species (Watts and Conley 1981). They should not be used to predict actual population parameters but instead should indicate a range of possibilities for those parameters (Fowler 1981). In discussing the role of computer simulations in wildlife science, Romesburg (1981) viewed these models as comprehensive tools for integrating knowledge, common sense, hunches, and opinions. It is in this role that we feel computer simulations can be an aid to estimating MVP size and minimum area requirements for endangered species. Shaffer's grizzly bear simulation is presently being used by wildlife managers in Montana and Wyoming in this capacity. In addition, an adaptation of his simulation is currently being made available to the USDA Forest Service for use in the management of vertebrate species in their forest planning process (Shaffer, personal communication).

Genetic Considerations

$$f = 1 - \left(1 - \frac{1}{2N_e}\right)^t$$

Increasing attention is being given to estimating minimum population numbers from a genetic standpoint (Soulé and Wilcox 1980, Frankel and Soulé 1981, Schonewald-Cox et al. 1983, Lacava and Hughes 1984, Lehmkühl 1984, Salwasser et al. 1984). The critical question is what population thresholds are necessary to maintain short-term and long-term (evolutionary) fitness. Based on the extensive experience of animal breeders, Franklin (1980) and Soulé (1980) determined that the maximum allowable rate of inbreeding necessary to avoid short-term effects of inbreeding depression is 1% per generation. This rule of thumb translates to a genetically effective size of 50 for maintenance of short-term fitness.

The concept of a genetically effective population (N_e) is important. Such a population is defined as one in which all individuals mate randomly, the sex ratio approaches unity, variance in family size is zero, and generations do not overlap. Obviously, few if any vertebrate populations meet these criteria. Thus, a genetically effective size of 50 translates into a larger actual (census) number of breeding adults for most species.

Several mathematical expressions have been derived for determining the effects of variance in progeny, unequal sex ratios, overlapping generations, and population fluctuations on the genetically effective population size (e.g., Kimura and Crow 1963, Emigh and Pollak 1979). Lehmkühl (1984) developed a procedure, based on the above formulae, for adjusting the genetically effective population of 50 to arrive at the census number of breeding animals. With Lehmkühl's procedure, we estimated the number of breeding ferrets (N) necessary to maintain a genetically effective population (N_e) of 50 (see the Appendix for calculations). Results of this exercise indicated that a MVP of 214 breeding ferrets is necessary for maintenance of short-term genetic fitness. This MVP estimate is five times the known number of adults in the Wyoming population (Forrest et al., in manuscript). Minimum area requirements for this MVP estimate would be about 10,700 ha of white-tailed prairie dog habitat.

A question arises as to what constitutes short-term versus long-term genetic fitness. This question can be satisfactorily answered with the following equation

where f equals the inbreeding coefficient, N_e equals the genetically effective population size, and t equals generation time. Animal breeders have noted a significant reduction in fecundity when f approaches 0.5–0.6 (Soulé 1980). Setting N_e at 50 and f at 0.6 in the above equation results in t equal to about 90 generations. If the generation time for the ferret is 1 year (time from birth of a female kit to birth of her first litter), it would take about 90 years for an effective population of 50 ferrets to reach an inbreeding coefficient that could cause extinction solely on genetic grounds. If the N_e for the Wyoming ferret population is now substantially less than 50 animals, this short-term genetic threshold could be reached in considerably fewer than 90 years. The amount of time the population has already been isolated may be several decades.

Franklin (1980) suggested that a genetically effective population of 500 animals is necessary for long-term genetic variation required by the evolutionary process. As with short-term fitness, a N_e of 500 translates into a much larger number of breeding adults when dealing with real, as opposed to ideal, populations. As an alternative to this rule of thumb approach, Frankel and Soulé (1981) suggested monitoring genetic variation in target species by electrophoretic techniques that estimate percentage polymorphisms and percentage heterozygosity in a population. Data from natural populations suggest that relatively heterozygous individuals have greater viability and fecundity than individuals with lower percentages of heterozygosity and polymorphism (Soulé 1980).

For many species, particularly endangered ones, electrophoretic techniques can be impractical for several reasons. First, they require potentially injurious tissue sampling. Second, small sample sizes of most studies can verify the presence but not the absence of rare alleles and preclude the use of statistics to test departures from Hardy-Weinburg frequencies. Third, many higher vertebrates lack polymorphic genetic markers that these techniques can detect. Nevertheless, if these techniques become more efficient and automated in the future, they could be a valuable management tool for working with threatened and endangered species. If test results indicated a reduction in genetic variability, then restorative steps, such as increasing N_e ,

could be taken (Frankel and Soulé 1981). Baseline data on genetic variation in the Wyoming ferret population are now being gathered (Kilpatrick et al., 1986).

Although both empirical data and theory have contributed to developing the genetic approach to estimating MVP size, this method is not without its shortcomings. Both the "50 and 500 rules" which are being advanced are based on simple, analytical models of population genetics that do not account for either age structure or environmental stochasticity. Previous work indicates that the exclusion of age structure can dramatically decrease MVP size (Shaffer 1978) and in so doing optimistically deflate the MVP estimates.

DISCUSSION AND CONCLUSION

At the outset of this paper, we indicated that the five methods for estimating MVP size would be evaluated in relation to research impacts on target species and the value of accurate and precise data when time is a critical factor. In the black-footed ferret study, we adopted the pragmatic philosophy of Frankel and Soulé (1981) that conservationists must often employ rough approximations of critical parameters instead of waiting for precise data that may never be obtained. Assuming that this philosophy is sound for most endangered species studies, in practice it leads us to conclude that the experimental and simulation methods for estimating MVP size have serious limitations. The former requires a lengthy study period, and the latter an extensive set of population data. Neither time nor extensive population data are goods in great supply for most endangered species programs. As previously pointed out, though, it should be possible at times to use less than "perfect" data in the simulation approach to produce a meaningful MVP estimate.

Although Shaffer (1981) underscored the importance of defining MVP size with explicit but flexible criteria (i.e., time frame and survival probability), only two of the five methods examined (T_k and simulation) yield results that include both of these criteria. Are we then to dismiss the other approaches as meaningless exercises? We think not. When applicable, both the experimental and biogeographical methods provide empirical data for estimating MVP size, although no survival probability can be attached to their estimates. A prudent path for any con-

servation biologist should be to use both empirical as well as theoretical approaches such as island biogeography and genetic considerations.

Each of the methods for estimating MVP size relies on several assumptions. Which method(s) then are most appropriate? Looking at this same question from another angle, one might ask to which type of perturbation is the target species or population most susceptible. For most endangered species, it is unlikely that the latter question will be answerable; it is likely that the target species will be subject to some combination of demographic, environmental, and genetic perturbations. Therefore, those methods that take into account these perturbations should probably carry the most weight. Obviously, the available data will also dictate to some extent which methods can be used.

For the majority of endangered species studies, empirical data necessary for estimating MVP size with the experimental and biogeographical methods will not be available. If population data on natality and mortality are obtainable, then a combination of the simulation and genetic approaches may yield the best estimate of MVP size. The simulation method can account for both demographic and environmental perturbations, and the genetic method can account for demographic stochasticity as it relates to genetic drift. On the other hand, theoretical methods like the T_k model of island biogeography only account for demographic perturbations. A combination of the simulation and genetic approaches will likely produce a range of MVP estimates. Results of the recent Forest Service workshop indicated that environmental and demographic variability may be more important than genetic variability in setting the lower limit to population viability (M. L. Shaffer, personal communication). One possible implication of these results is that the final MVP estimate should be biased toward that estimate produced by the simulation method. However, management constraints will also be a primary factor in establishing MVP size somewhere within the range of estimates.

When no population data are available and empirical approaches have also been ruled out, then genetic considerations must take priority in estimating MVP size. This is the case for the ferret. Until more data are obtained for simulations, we must rely on our estimate of about 200

animals by the genetics method to serve as the MVP estimate for black-footed ferrets. In the final analysis, this number may be reduced as a result of compromising between estimates from the simulation and genetics methods.

The preceding discussion on genetic approaches is relevant only to maintenance of short-term fitness. For fitness on a long-term scale, we must try to establish several ferret populations, each of which maintains a short-term MVP size. Although such goals may now appear beyond the vision of what resource managers can do to conserve the ferrets in the near term, we must never lose sight of the fact that large, viable populations of ferrets and other endangered species are necessary for the recovery and conservation of these species from an evolutionary standpoint.

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APPENDIX

Calculation of actual adult census number (N) for black-footed ferrets through adjustment of genetically effective population size (N_e) (Lehmkühl 1984).

Step 1: Adjustment for variation in progeny number.

$$N = (2N_e V_k + 1)/K^2$$

where N_e = effective population size of 50, V_k = variance in number of young, K = mean number of young per female. When lacking data on V_k , multiply 1.4 times N_e . For the black-footed ferret: $50 \times 1.4 = 70$.

Step 2: Adjustment for unequal sex ratio.

$$N_m = (N_e + [\text{male:female ratio} \times N_e])/4$$

where N_m = number of males.

$$N_f = N_m \times \text{female:male ratio}$$

$$N = N_m + N_f$$

$$N/50 = \text{increase in } N_e$$

$$N = \text{increase} \times 70 (\text{from Step 1})$$

For the black-footed ferret: (sex ratio data from 1984 census—Forrest et al., in manuscript)

$$N_m = (50 + 18/25(50))/4 = 21.5$$

$$N_f = 21.5 \times 25/18 = 29.9$$

$$N = 29.9 + 21.5 = 51.4$$

$$51.4/50 = 1.02$$

$$1.02 \times 70 = 71.4$$

Step 3: Adjustment for overlapping generation.

Double the census number from Step 2.

$$\text{For the black-footed ferret: } 2 \times 71.4 = 142.8$$

Step 4: Adjustment for population fluctuations.

Ratio between empirical high and low population censuses indicates factor with which to increase Step 3 result for MVP estimate.

$$\text{For black-footed ferret: } 43/28 = 1.5 \quad 1.5 \times 142.8 = 214$$

= MVP (1983 census = 28 adults, 1984 = 43, Forrest et al., in manuscript)

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